

Bark Spore Bank of Ferns in a Gallery Forest of the Ecological Station of Panga, Uberlândia–MG, Brazil

MARLI A. RANAL

Instituto de Biologia, Universidade Federal de Uberlândia,
Caixa Postal 593, 38400-902, Uberlândia, MG, Brasil

MISSOURI BOTANICAL

AUG 05 2004

GARDEN LIBRARY

ABSTRACT.—Information about fern spore banks is restricted to the soil systems. As the dispersion of spores occurs by means of air, it is possible to have viable spores on tree bark. Thus, it is important to know if on this kind of substrate, which is thinner and apparently more susceptible to desiccation than the soil, the spores can survive for any length of time, forming transient or persistent spore banks. Samples of bark were collected from ten angiosperm trees in March 1997 and from fifteen trees in February and September 1998. The samples collected in March 1997 contained from 0.05 to 7.19 gametophytes cm^{-2} of cultured bark, those of February 1998 from 0.11 to 4.22 gametophytes cm^{-2} , and in September 1998 from 0.32 to 5.0 gametophytes per square cm. Although the cerrado region is characterized by climatic seasonality, this seasonality was not observed in relation to number of viable spores on barks. As a consequence of the casual spore dispersion pattern, the bark spore bank has a random distribution among the trunks. Ten species were identified on barks collected in February 1998 and fifteen in September 1998, one of them epiphytic (*Phlebodium areolatum* (Humb. & Bonpl. ex Willd.) J. Sm.) and the others terrestrial species. *Thelypteris* was the most frequent genus in the analyzed samples. The results obtained show the potential for these substrates to retain viable spores that can participate in the regeneration process and population dynamics of the pteridophyte flora. Moreover, the existence of viable spores of terrestrial species on tree bark does not answer an important question—why do terrestrial species not establish themselves on trees?

Information about fern spore banks is restricted to the soil (Carroll and Ashton, 1965; Wee, 1974; Strickler and Edgerton, 1976; Pérez-García *et al.*, 1982; During and ter Horst, 1983; During *et al.*, 1987; Leck and Simpson, 1987; Hamilton, 1988; Lindsay and Dyer, 1990; Milberg, 1991; Dyer and Lindsay, 1992; Milberg and Anderson, 1994; Penrod and McCormick, 1996; Raffaele, 1996; Schneller and Holderegger, 1996; Simabukuro *et al.*, 1998, 1999; Ranal, 2003). As the dispersion of spores occurs by means of the air, it is possible that viable spores present on the bark of trees could germinate under appropriate conditions. Thus, it is important to know if on this kind of substrate, which is thinner and apparently more susceptible to desiccation than soil, the spores can survive long enough to form a transient or persistent bank. These spores can participate in the population dynamics, particularly of epiphyte species. The role of these fern spores could be amplified after the fall of trees, if spores of terrestrial species could survive in this kind of substrate. In vertical position the spore reception is maximized on the trunks. On the other hand, in horizontal positions (dead trees), wind action and self-defense of trees decreases. As a consequence, water retention and decomposition activities increase, making the germination process on this new substrate easier. In this sense, it will be possible to consider that this bark spore bank has the same role recognized for soil spore bank, that is, this bank could take an important role in

propagation and in preservation of fern species as pointed out for soil spore bank by Lindsay *et al.* (1992), Dyer (1994), and Dyer and Lindsay (1996); in sexual process and in genetic variability (Milberg, 1991); and in regeneration process of forest gaps.

In this context, the aim of this study was to investigate the existence of a bark spore bank on trunks of angiosperm trees in the gallery forest of the Ecological Station of Panga, Uberlândia-MG, Brazil. This being the case, the purpose was to characterize this bank in relation to quantity of viable spores and fern species composition.

MATERIALS AND METHODS

Bark was collected from ten angiosperm trees in March 1997, and from fifteen in February and September 1998. These trees are growing in the gallery forest of the Ecological Station of Panga, Uberlândia, Minas Gerais, Brazil, situated at 19°09'20"–19°11'10" S, 48°23'20"–48°24'35" W, at an elevation of approximately 800 m. This Station has 409.5 ha occupied by cerrado *sensu lato* (Schiavini and Araújo, 1989; Ratter, 1992). The region is characterized by an Aw climatic pattern (Köppen, 1948) with a wet and hot season from October to March and a dry and cold season from April to September (Ranal, 2003). Random sampling was used to mark the trees for the bark collection. All trees were adult individuals, with more than 15 cm in circumference at 1.30 m height and with sufficient bark to extract by scratching with a knife, without reaching live tissues. It means that dead bark was extracted (outer bark or rhytidome according to Esau, 1977), a perennial rhytidome with slow detachment. Bark samples were collected at about 1.30 m height around the trunks. As in 1998 the two collections were done on the same trees, the bark extraction was done at about 1.30 m height in February and at about 1.50 m in September.

After collection, each bark sample was placed in a plastic bag which was labelled and immediately closed to prevent contamination. In the laboratory bark samples were manually mixed and converted into small pieces and powder, inside the bags. Each bark sample was divided into sub-samples and spread over sterile sand in quadrangular, transparent, covered plastic boxes of 50 cm³ (experimental units), moistened with nystatin suspension (10,000 units nystatin per mL in DPBS—Dulbecco's Phosphate Buffered Saline; 1 mL per 100 mL of distilled water) and later, if necessary, with distilled water. Near the end of the experiments, when young sporophytes presented the first signals of chlorosis, the cultures were moistened with nutrient solution (Meyer *et al.*, 1963). Each experimental unit received 15 g of sterile sand and 1 g of bark. This quantity of bark formed a layer of approximately 5 mm thickness. Samples were maintained at 20.9–23.2°C, $35.77 \pm 6.71 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR (mean \pm standard deviation) for the March 1997 collection, at 21.4–24.4°C, $35.77 \pm 6.71 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR for the February 1998 collection, and at 21.8–22.9°C, $30.84 \pm 6.09 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR for the September 1998 collection. All samples were subjected to continuous white fluorescent light. Radiation measurements were made using a LI-COR LI-250 light meter and a LI-190SA quantum sensor.

Sterilized soil samples (10 replicates) were maintained under the same manipulation conditions to assess the level of contamination by foreign spores. The superficial area of cultured barks was used to calculate the number of gametophytes and sporophytes formed per square centimeter. As bryophytes were the first colonizer of the barks, fern gametophytes were counted 2–3 months after each collection, when they reached adult form, becoming easily visible.

The number of gametophytes formed was the criterion used to evaluate viable spores on the bark samples. Sporophytes were counted when cultures were two (February collection) or three months old (March and September collections). The criterion to count sporophytes was the presence of a perceptible crozier when viewed under stereomicroscope. At the end of the experiments young sporophytes were transplanted to bags containing soil and were maintained under greenhouse conditions until the production of fertile leaves when they were collected. The sporophytes collected were prepared and deposited at HUFU and SP.

The experimental units were randomly distributed in laboratory conditions, with two sub-samples per tree for March 1997 collection (20 cells) and four subsamples per tree for February and September 1998 collection (60 cells for each collection date). The number of gametophytes and sporophytes formed per square centimeter of cultured bark, as well as the percentage of gametophytes forming sporophytes were submitted to the Shapiro-Wilk (normality of populations) and Bartlett or Cochran tests (homogeneity between variances). If the original data exhibited normality and homogeneity, they were submitted to analysis of variance and Tukey test. If the original and transformed data showed non-normality and/or heteroscedasticity, non-parametric statistical tests were used (Kruskal-Wallis and Wilcoxon-Mann-Whitney tests). Comparisons between the bark spore bank of the wet and dry seasons were carried out using the Mann-Whitney test. Pearson correlations were made to detect associations between number of gametophytes formed on cultured barks and tree characteristics (height, circumference, N, P, K, Ca, Mg, S, Fe, B, Cu, Mn, and Zn content).

Bark samples collected were chemically analyzed in the Laboratory of Leaf Analysis of the Federal University of Uberlândia, according to Miyazawa *et al.* (1999).

RESULTS

All analyzed trees presented viable spores in their outer bark (Tables 1–3). The size of the bark spore bank, evaluated in relation to gametophytes formed, varied from 0.05 to 7.19 gametophytes cm^{-2} of cultured bark. There is no seasonality in the bark spore bank (Table 4). Half of the analyzed trees showed no differences between February (wet season) and September (dry season) collections; three showed increase in number of viable spores and four showed decrease in number of viable spores at the end of the dry season. There is no association between angiosperm species, tree size or chemical composition of the bark and the number of viable spores on barks (Tables 1–3, 5, 6). The same

TABLE 1. Gametophytes and sporophytes formed per square centimeter of cultured barks of angiosperms occurring in a gallery forest of Ecological Station of Panga, Uberlândia-MG, Brazil and their reproductive success measured by percentage of gametophytes forming sporophytes (mean \pm standard deviation). March 1997 collection.

Angiosperm Species	Family	Gametophytes cm ⁻²	Sporophytes cm ⁻²	% sporophytes
<i>Psidium rufum</i> Mart. ex DC. ⁽¹⁾	Myrtaceae	7.19 \pm 0.49 a	2.68 \pm 0.38 a	37.24 \pm 2.76 ab
tree in decomposition	—	2.15 \pm 0.30 b	0.82 \pm 0.43 b	39.82 \pm 25.56 ab
<i>Luehea divaricata</i> Mart.	Tiliaceae	1.93 \pm 0.41 bc	0.37 \pm 0.23 b	18.16 \pm 8.00 ab
tree in decomposition	—	1.56 \pm 0.47 bcd	0.33 \pm 0.20 b	20.19 \pm 6.80 ab
Unidentified sp. ⁽¹⁾	—	0.89 \pm 0.87 bcd	0.00 \pm 0.00 b	0.00 \pm 0.00 b
<i>Cupania vernalis</i> Cambess.	Sapindaceae	0.59 \pm 0.22 bcd	0.00 \pm 0.00 b	0.00 \pm 0.00 b
<i>Chrysophyllum marginatum</i> Radlk.	Sapotaceae	0.48 \pm 0.005 cd	0.05 \pm 0.07 b	10.00 \pm 14.14 b
undentified sp. ⁽¹⁾	—	0.49 \pm 0.39 cd	0.29 \pm 0.26 b	56.25 \pm 8.84 a
<i>Matayba guianensis</i> Aubl.	Sapindaceae	0.09 \pm 0.0 d	0.00 \pm 0.00 b	0.00 \pm 0.00 b
<i>Terminalia brasiliensis</i> Eichl.	Combretaceae	0.05 \pm 0.07 d	0.00 \pm 0.00 b	0.00 \pm 0.00 b
W		0.9813	0.9433	0.9301
Cochran		0.4473	0.3718	0.6227
F _{9; 10}		53.29**	27.55**	7.78**

W: Shapiro-Wilk test ($\alpha = 0.05$); boldfaced values indicate normality of populations ($P > 0.05$). Boldface values for Cochran test indicate homogeneity between variances. F: value of Snedecor's distribution, including the degrees of freedom; ** $P \leq 0.01$. Means followed by the same letter in each column are not significantly different based on the Tukey test ($\alpha = 0.05$). ¹ Tree with *Microgramma persicariifolia*.

angiosperm species presented high or low number of viable spores, trees with different dimensions presented similar number of viable spores without any significant correlation between tree size and bark bank size, and weak tendency related to chemical composition could be observed. Moderate to substantial negative correlations (Table 6), according to the criterion adopted by Miller (1994), were detected for nitrogen (February collection), magnesium, and copper content (September collection).

Sporophyte production ranged from zero to 2.68 sporophytes cm⁻² of cultured bark and the reproductive success (percentage of gametophytes forming sporophytes) from zero to 62.10 % (Tables 1–3).

Host trees of viable fern spores are presented on table 7. Ten fern species were recognized in barks collected in February 1998 and 15 species in barks collected in September 1998. Each analyzed tree presented from two to ten fern species in their barks. *Pityrogramma calomelanos* (L.) Link var. *calomelanos* and *Thelypteris opposita* (Vahl) Ching were broadly distributed, occurring in 13 trees, from the 25 analyzed; *Phlebodium areolatum* (Humb. & Bonpl. ex Willd.) J. Sm., *Pteris vittata* L., *Thelypteris burkartii* Abbiatti, and *T. mosenii* (C. Chr.) C.F. Reed appeared only in one tree. *Phlebodium areolatum* is epiphyte and the others are terrestrial species. *Microgramma persicariifolia* (Schrad.) Presl was found growing as an epiphyte in the forest, but no

TABLE 2. Gametophytes and sporophytes formed per square centimeter of cultured barks of angiosperms occurring in a gallery forest of Ecological Station of Panga, Uberlândia-MG, Brazil and their reproductive success measured by percentage of gametophytes forming sporophytes (mean \pm standard deviation). February 1998 collection.

Angiosperm Species	Family	Gametophytes cm ⁻²	Sporophytes cm ⁻²⁽¹⁾	% sporophytes
<i>Copaifera langsdorffii</i> Desf. ⁽²⁾	Caesalpiniaceae	4.22 \pm 0.42 a	2.29 \pm 0.30 a	54.22 \pm 2.51 a
<i>Eugenia ligustrina</i> Miq.	Myrtaceae	2.80 \pm 0.42 ab	1.22 \pm 0.23 b	43.78 \pm 6.54 ab
<i>Endlicheria paniculata</i> (Spreng.) Macbride ⁽³⁾	Lauraceae	2.68 \pm 0.99 ab	1.59 \pm 0.70 ab	58.67 \pm 10.36 a
<i>Eugenia ligustrina</i>	Myrtaceae	2.26 \pm 0.54 abc	0.91 \pm 0.32 bc	40.86 \pm 12.94 ab
<i>Aspidosperma</i> <i>cylindrocarpum</i> Muell. Arg.	Apocynaceae	2.06 \pm 0.36 abc	0.51 \pm 0.14 cd	24.70 \pm 4.41 ab
<i>Tapirira guianensis</i> Aubl.	Anacardiaceae	1.94 \pm 0.54 abc	0.91 \pm 0.20 bc	49.07 \pm 15.61 ab
<i>Coussarea hydrangeae-</i> <i>folia</i> Benth. & Hook. f.	Rubiaceae	1.92 \pm 0.59 abc	0.32 \pm 0.14 def	16.76 \pm 6.59 ab
<i>Eugenia florida</i> DC.	Myrtaceae	1.55 \pm 0.57 abc	0.28 \pm 0.11 def	19.64 \pm 8.27 ab
<i>Inga affinis</i> DC.	Mimosaceae	1.49 \pm 0.30 abc	0.45 \pm 0.16 cde	30.27 \pm 6.32 ab
<i>Luehea divaricata</i> Mart. dead tree	Tiliaceae —	1.32 \pm 0.22 abc 0.83 \pm 0.39 bc	0.56 \pm 0.09 cd 0.02 \pm 0.04 f	43.14 \pm 7.94 ab 1.56 \pm 3.12 b
<i>Tapirira guianensis</i> <i>Aspidosperma</i> <i>cylindrocarpum</i>	Anacardiaceae Apocynaceae	0.75 \pm 0.29 bc 0.50 \pm 0.08 bc	0.32 \pm 0.22 def 0.15 \pm 0.11 def	44.17 \pm 24.10 ab 29.64 \pm 21.61 ab
<i>Tapirira guianensis</i>	Anacardiaceae	0.17 \pm 0.10 c	0.02 \pm 0.04 f	25.00 \pm 50.0 ab
<i>Luehea divaricata</i>	Tiliaceae	0.11 \pm 0.11 c	0.06 \pm 0.08 ef	41.67 \pm 50.0 ab
W		0.9435	0.9728	0.8774
Bartlett		—	24.1624	—
F _{14; 45}		—	31.42**	—
H		52.11**	—	30.32**

W: Shapiro-Wilk test ($\alpha = 0.05$); boldfaced value indicates normality of populations ($P > 0.05$). Boldface value for Bartlett test indicates homogeneity between variances. F: value of Snedecor's distribution, including the degrees of freedom; ** $P \leq 0.01$. H: Kruskal-Wallis test; ** $P \leq 0.01$. Means followed by the same letter in each column are not significantly different based on the Wilcoxon-Mann-Whitney or Tukey test ($\alpha = 0.05$). ¹ Data submitted to square root plus 0.5 transformation for the adjustment to normality and homogeneity; means and standard deviation are original numbers; numbers and letters related to statistics are based on transformed data. ² Tree with *Microgramma persicariifolia*. ³ Bark collected of the horizontal part of the stem.

gametophyte of this species was found in the analyzed barks. *Thelypteris* was the most frequent genus among the analyzed samples (Table 8).

DISCUSSION

The bark spore bank of the analyzed trees is smaller than the soil spore bank of the middle and edge of the same gallery forest, at the first centimeters of the soil column (2–7 cm depth), in the wet season, and similar to that soil spore bank in deeper soil column (15–22 cm depth). Soil samples of the gallery forest of the Ecological Station of Panga could reach 29.52 gametophytes cm⁻² of

TABLE 3. Gametophytes and sporophytes formed per square centimeter of cultured barks of angiosperms occurring in a gallery forest of Ecological Station of Panga, Uberlândia-MG, Brazil and their reproductive success measured by percentage of gametophytes forming sporophytes (mean \pm standard deviation). September 1998 collection.

Angiosperm Species	Family	Gametophytes cm ⁻²	Sporophytes cm ⁻²	% sporophytes
<i>Copaifera langsdorffii</i> Desf. ⁽¹⁾	Caesalpiniaceae			46.81 \pm 8.80 a
		2.52 \pm 0.32 ab	1.18 \pm 0.22 b	
<i>Eugenia ligustrina</i> Miq.	Myrtaceae	0.83 \pm 0.36 bc	0.23 \pm 0.10 d	29.38 \pm 15.60 a
<i>Endlicheria paniculata</i> (Spreng.) Macbride ⁽²⁾	Lauraceae			37.12 \pm 7.82 a
		5.00 \pm 0.73 a	1.86 \pm 0.53 a	
<i>Eugenia ligustrina</i>	Myrtaceae	0.73 \pm 0.39 bc	0.26 \pm 0.19 d	35.02 \pm 13.54 a
<i>Aspidosperma</i> <i>cylindrocarpum</i> Muell. Arg.	Apocynaceae			30.15 \pm 17.84 a
		1.54 \pm 0.35 abc	0.45 \pm 0.26 cd	
<i>Tapirira guianensis</i> Aubl.	Anacardiaceae	1.75 \pm 0.50 abc	1.02 \pm 0.23 bc	62.10 \pm 25.65 a
<i>Coussarea hydrangeaefolia</i> Benth. & Hook. f.	Rubiaceae			14.45 \pm 14.08 a
		0.93 \pm 0.28 bc	0.11 \pm 0.09 d	
<i>Eugenia florida</i> DC.	Myrtaceae	1.30 \pm 0.05 abc	0.70 \pm 0.28 bcd	54.06 \pm 21.82 a
<i>Inga affinis</i> DC.	Mimosaceae	1.95 \pm 0.43 abc	0.24 \pm 0.15 d	14.09 \pm 11.86 a
<i>Luehea divaricata</i> Mart.	Tiliaceae	2.47 \pm 0.49 ab	1.10 \pm 0.56 bc	46.54 \pm 25.60 a
dead tree	—	2.28 \pm 1.45 abc	0.70 \pm 0.24 bcd	34.78 \pm 13.26 a
<i>Tapirira guianensis</i>	Anacardiaceae	0.88 \pm 0.12 bc	0.52 \pm 0.24 bcd	58.61 \pm 20.19 a
<i>Aspidosperma</i> <i>cylindrocarpum</i>	Apocynaceae			56.75 \pm 15.61 a
		1.84 \pm 0.36 abc	1.00 \pm 0.13 bc	
<i>Tapirira guianensis</i>	Anacardiaceae	0.43 \pm 0.29 c	0.13 \pm 0.11 d	30.42 \pm 27.50 a
<i>Luehea divaricata</i>	Tiliaceae	0.32 \pm 0.19 c	0.17 \pm 0.12 d	47.5 \pm 41.13 a
W		0.9078	0.9708	0.9837
Bartlett		—	23.9762	14.8281
F _{14; 45}		—	14.1975**	2.1431*
H		51.6850**	—	—

W: Shapiro-Wilk test ($\alpha = 0.05$); boldfaced values indicate normality of populations ($P > 0.05$).

cultured soil, in the wet season, when collected at 2–4 cm depth, and ranged from 0.13 to 6.84 gametophytes cm⁻² from 15 to 22 cm depth (Ranal, 2003). Dyer and Lindsay (1992) registered more than 30 gametophytes cm⁻² from surface to 2.5 cm depth of soil collected in North Carolina and 0.46 gametophytes cm⁻² at 20.0–22.5 cm.

Similar results in relation to reproductive success were obtained for soil spore bank studies (0.76 to 63.33 % gametophytes producing sporophytes) of the same gallery forest (Ranal, 2003).

Periodic observations indicate that for some species of the Ecological Station of Panga, production of new leaves occurs in October–November, at the beginning of the rainy season, and the production of fertile leaves occurs in

TABLE 4. Simple comparisons for gametophytes formed in bark samples collected in February and September 1998, in the gallery forest, Ecological Station of Panga, Uberlândia-MG. The mean values and the dispersion measurements are included on tables 2 and 3.

Angiosperm Species	U value	P value
<i>Copaifera langsdorffii</i> Desf.	16.0	0.0286
<i>Eugenia ligustrina</i> Miq.	16.0	0.0286
<i>Endlicheria paniculata</i> (Spreng.) Macbride	16.0	0.0286
<i>Eugenia ligustrina</i>	16.0	0.0286
<i>Aspidosperma cylindrocarpum</i> Muell. Arg.	14.0	0.1140
<i>Tapirira guianensis</i> Aubl.	8.5	0.8860
<i>Coussarea hydrangeaefolia</i> Benth. & Hook. f.	16.0	0.0286
<i>Eugenia florida</i> DC.	8.0	1.0000
<i>Inga affinis</i> DC.	13.0	0.2000
<i>Luehea divaricata</i> Mart.	16.0	0.0286
dead tree	15.0	0.0571
<i>Tapirira guianensis</i>	11.0	0.4860
<i>Aspidosperma cylindrocarpum</i>	16.0	0.0286
<i>Tapirira guianensis</i>	14.0	0.1140
<i>Luehea divaricata</i>	12.0	0.3430

U: statistic of the Mann-Whitney test. P: probability to accept or reject the null hypothesis. $P > 0.05$ means that the two medians are not significantly different. $P < 0.05$ means that the two medians are significantly different.

December–January. Spore dispersal occurs from December for precocious leaves to March–April for late leaves, depending on the annual rainfall distribution. This seasonality in spore production was not observed in the bark spore bank, but was detected for soil spore bank in the first centimeters of soil

TABLE 5. Bark chemical composition of angiosperm species occurring in the gallery forest of Ecological Station of Panga, Uberlândia-MG, Brazil.

Angiosperm Species	g Kg ⁻¹						mg Kg ⁻¹				
	N	P	K	Ca	Mg	S	Fe	B	Cu	Mn	Zn
<i>Aspidosperma</i>											
<i>cylindrocarpum</i> Muell. Arg.	17.2	1.2	1.5	8.6	1.2	1.9	17508.0	15.0	18.0	252.0	23.0
<i>Aspidosperma cylindrocarpum</i>	19.0	1.5	1.5	10.3	1.3	2.0	15030.0	26.0	17.0	203.0	21.0
<i>Copaifera langsdorffii</i> Desf.	11.4	0.9	1.5	4.5	1.0	1.3	11503.0	23.0	13.0	350.0	20.0
<i>Coussarea hydrangeaefolia</i>											
Benth. & Hook. f.	13.9	0.9	0.5	7.7	0.8	1.1	6015.0	17.0	10.0	703.0	15.0
<i>Endlicheria paniculata</i>											
(Spreng.) Macbride	15.4	1.5	2.0	6.8	1.1	2.1	27000.0	17.0	25.0	1051.0	61.0
<i>Eugenia florida</i> DC.	12.1	0.8	1.5	26.8	1.2	1.4	16005.0	21.0	11.0	293.0	42.0
<i>Eugenia ligustrina</i> Miq.	13.5	0.7	1.0	24.9	1.6	1.3	7012.0	18.0	12.0	125.0	22.0
<i>Eugenia ligustrina</i>	12.1	0.7	1.0	20.8	1.2	1.0	6511.0	13.0	10.0	133.0	22.0
<i>Inga affinis</i> DC.	16.1	1.7	7.0	10.6	1.7	2.1	27000.0	21.0	25.0	675.0	40.0
<i>Luehea divaricata</i> Mart.	13.9	0.8	1.0	48.3	3.6	1.4	10000.0	11.0	17.0	1105.0	240.0
<i>Luehea divaricata</i>	15.7	0.9	1.0	43.3	2.3	0.9	16550.0	18.0	25.0	551.0	115.0
<i>Tapirira guianensis</i> Aubl.	13.2	0.8	1.0	43.9	1.9	1.0	5750.0	28.0	15.0	425.0	20.0
<i>Tapirira guianensis</i>	15.4	1.2	1.5	25.2	1.9	2.0	2250.0	23.0	22.0	675.0	55.0
<i>Tapirira guianensis</i>	13.9	0.9	1.0	26.8	2.6	1.0	5020.0	18.0	15.0	148.0	23.0
dead tree	11.7	0.8	3.0	19.3	1.1	0.9	7750.0	22.0	8.0	177.0	47.0

TABLE 6. Coefficients of the linear correlation (r) among tree characteristics and gametophytes per square centimeter of cultured bark collected in February and September 1998 in the gallery forest of the Ecological Station of Panga, Uberlândia-MG, Brazil.

Tree characteristics	r values ¹	P values	r values ²	P values
Height (m)	-0.1014	0.3596	0.0932	0.3706
Circumference (cm)	0.1580	0.2869	0.0728	0.3983
N	-0.5003	0.0288	-0.3538	0.0979
P	-0.1228	0.3314	-0.1615	0.2827
K	0.3403	0.1073	0.0634	0.4112
Ca	-0.2815	0.1548	-0.0691	0.4033
Mg	-0.3348	0.1113	-0.4716	0.0380
S	-0.0176	0.4752	-0.0736	0.3971
Fe	0.1775	0.2634	0.0889	0.3763
B	-0.0678	0.4051	0.2245	0.2106
Cu	-0.3978	0.0710	-0.4591	0.0426
Mn	0.0298	0.4581	-0.2133	0.2227
Zn	0.0817	0.3861	-0.2651	0.1698

¹ linear correlation for gametophytes per square centimeter of cultured bark collected in February 1998. ² linear correlation for gametophytes per square centimeter of cultured bark collected in September 1998. $P > 0.05$ means that null hypothesis was accepted and r was not considered as significantly different from zero by "Student's" t test. $P < 0.05$ means that null hypothesis was rejected and r was considered as significantly different from zero by "Student's" t test.

column, with high quantity of viable spores occurring at the end of the wet season and low quantity at the end of the dry season (Ranal, 2003).

Although *Copaifera langsdorffii* Desf. contains alkaloids and terpenoids in its bark (Souza and Silva, 2001), these substances apparently did not influenced the spore germination and gametophyte development of *Pityrogramma calomelanos* var. *calomelanos*, *Pteridium aquilinum* (L.) Kuhn var. *arachnoideum* (Kaulf.) Brade, *Thelypteris burkartii*, *T. conspersa* (Schrad.) A. R. Sm., *T. dentata* (Forssk.) E. St. John, *T. hispidula* (Decne) C. F. Reed, *T. opposita* (Vahl) Ching, and *T. patens* (Sw.) Small because viable spores of these species were maintained on its bark, with normal development until sporophyte production. Alkaloids and terpenoids are related to allelopathic mechanisms that inhibit the germination process (Inderjit and Dakshini, 1995).

Five of the species of the bark spore bank did not occur in soil samples of the gallery forest of the Panga Stream (*Phlebodium areolatum*, *Pityrogramma trifoliata* (L.) R.M. Tryon, *Pteridium aquilinum* var. *arachnoideum*, *Pteris vittata*, and *Thelypteris burkartii*). On the other hand, three of the 13 species registered by Ranal (2003) in the soil of the gallery forest of Panga did not occur in bark cultures (*Lygodium venustum* Sw., *Blechnum brasiliense* Desv., and *Blechnum occidentale* L.). Thus, there were 10 common species in the soil and bark spore bank.

The interpretation of these data is limited because these are the first results about bark spore banks and few angiosperm species were analyzed. Moreover, there is no assurance that all fern spores present on the barks could germinate and form sporophytes under the experimental conditions used in this study. Several environmental factors such as wind currents, rainfall, gravity, and

TABLE 7. Species that are able to form bark spore bank in the gallery forest of the Ecological Station of Panga, Uberlândia, MG.

Fern species	Host tree
<i>Macrothelypteris torresiana</i> (Gaud.) Ching	<i>Coussarea hydrangeaefolia</i> Benth. & Hook. f. dead tree <i>Eugenia florida</i> DC. <i>Inga affinis</i> DC. <i>Luehea divaricata</i> Mart. <i>Tapirira guianensis</i> Aubl. <i>Tapirira guianensis</i>
<i>Phlebodium areolatum</i> (Humb. & Bonpl. ex Willd.) J. Sm.	
<i>Pityrogramma calomelanos</i> (L.) Link var. <i>calomelanos</i>	<i>Aspidosperma cylindrocarpum</i> Muell. Arg. <i>Copaifera langsdorffii</i> Desf. <i>Coussarea hydrangeaefolia</i> dead tree <i>Endlicheria paniculata</i> (Spreng.) Macbride <i>Eugenia florida</i> <i>Eugenia ligustrina</i> Miq. <i>Inga affinis</i> <i>Luehea divaricata</i> <i>Tapirira guianensis</i>
<i>Pityrogramma trifoliata</i> (L.) R. M. Tryon	<i>Aspidosperma cylindrocarpum</i> dead tree <i>Endlicheria paniculata</i> <i>Eugenia ligustrina</i> <i>Inga affinis</i> <i>Luehea divaricata</i> <i>Tapirira guianensis</i>
<i>Pteris vittata</i> L.	<i>Tapirira guianensis</i>
<i>Pteridium aquilinum</i> (L.) Kuhn var. <i>arachnoideum</i> (Kaulf.) Brade	<i>Copaifera langsdorffii</i> <i>Endlicheria paniculata</i> <i>Eugenia ligustrina</i> <i>Inga affinis</i> <i>Tapirira guianensis</i>
<i>Thelypteris burkartii</i> Abbiatti	<i>Copaifera langsdorffii</i>
<i>Thelypteris conspersa</i> (Schrad.) A. R. Sm.	<i>Aspidosperma cylindrocarpum</i> <i>Copaifera langsdorffii</i> <i>Endlicheria paniculata</i> <i>Eugenia florida</i> <i>Inga affinis</i> <i>Luehea divaricata</i> <i>Tapirira guianensis</i>
<i>Thelypteris dentata</i> (Forssk.) E. St. John	<i>Copaifera langsdorffii</i> dead tree <i>Endlicheria paniculata</i> <i>Eugenia florida</i> <i>Eugenia ligustrina</i> <i>Tapirira guianensis</i>
<i>Thelypteris hispidula</i> (Decne) C.F. Reed	<i>Aspidosperma cylindrocarpum</i> <i>Copaifera langsdorffii</i> dead tree

TABLE 7. Continued.

Fern species	Host tree
	<i>Endlicheria paniculata</i>
	<i>Eugenia ligustrina</i>
	<i>Inga affinis</i>
	<i>Luehea divaricata</i>
	<i>Tapirira guianensis</i>
<i>Thelypteris interrupta</i> (Willd.) Iwats.	<i>Aspidosperma cylindrocarpum</i>
	<i>Eugenia florida</i>
	<i>Eugenia ligustrina</i>
	<i>Tapirira guianensis</i>
<i>Thelypteris mosenii</i> (C. Chr.) C.F. Reed	dead tree
<i>Thelypteris opposita</i> (Vahl) Ching	<i>Aspidosperma cylindrocarpum</i>
	<i>Copaifera langsdorffii</i>
	<i>Coussarea hydrangeaefolia</i>
	dead tree
	<i>Endlicheria paniculata</i>
	<i>Eugenia florida</i>
	<i>Eugenia ligustrina</i>
	<i>Inga affinis</i>
	<i>Luehea divaricata</i>
	<i>Tapirira guianensis</i>
<i>Thelypteris patens</i> (Sw.) Small	<i>Aspidosperma cylindrocarpum</i>
	<i>Copaifera langsdorffii</i>
	<i>Luehea divaricata</i>
	<i>Tapirira guianensis</i>
<i>Thelypteris</i> sp.	<i>Coussarea hydrangeaefolia</i>
	<i>Eugenia florida</i>
	<i>Eugenia ligustrina</i>
	<i>Luehea divaricata</i>
	<i>Tapirira guianensis</i>

temperature can participate in the spore dispersion (Page, 1979) and several factors act in the trees, modifying their barks and preparing them to shelter epiphytes (Barkman, 1958). Among them are light affecting the temperature and evaporation, rainfall, atmospheric humidity, and characteristics of the trees such as water and vapour capacity of bark, colour influencing the warmth capacity, hardness, presence of fissures, acidity and chemical composition of the bark. As no association between the size of this spore bank and angiosperm species, tree dimensions or chemical composition of the bark was observed, perhaps the wealth or poverty of these trees in relation to the number of viable spores depends on the dispersal spore processes as an important factor. As a consequence of the casual spore dispersion pattern, the bark spore bank has a random distribution among the trunks. The influence of the physical characteristics of the outer bark needs to be studied for a complete understanding of this bank.

The data obtained in this study show that barks retain viable spores that can participate in the regeneration process and population dynamics of the environment. Probably the spores with greater longevity could participate in

the recomposition processes mentioned above when the tree falls on the soil. In this sense, the participation of the spores included in the soil in these processes can be higher than that included in the barks. The greater quantity of spores on the soil surface and the infrequent fall of trees in the studied forest make the establishment of gametophytes and sporophytes arising from the soil spore bank faster than those originating from bark spore bank.

The existence of viable spores of terrestrial species on tree bark does not answer an important question—Why do terrestrial species not establish themselves on trees?

ACKNOWLEDGMENTS

Statistical information and suggestions were provided by Dr. Denise G. Santana and Paulo Rangearo Peres. The identifications of the species were done by Dr. Jefferson Prado and the confirmations of some *Thelypteris* species by Dr. Alan R. Smith and Dr. M. Monica Ponce. The field work was done with the help of Mr. Hélio Pereira. Review of the English text was done by Mr. John David Bagnall. Important constructive criticism was done by the anonymous referees and by Dr. James Hickey. The author registers her sincere thanks.

LITERATURE CITED

- BARKMAN, J. J. 1958. *Phytosociology and ecology of cryptogamic epiphytes: including a taxonomic survey and description of their vegetation units in Europe*. Van Gorcum & Comp. N.V., Assen.
- CARROLL, E. J. and D. H. ASHTON. 1965. Seed storage in soils of several Victorian plant communities. *Victorian Naturalist* 82:102–110.
- DURING, H. J., M. BRUGUÉS, R. M. CROS and F. LLORET. 1987. The diaspore bank of bryophytes and ferns in the soil in some contrasting habitats around Barcelona, Spain. *Lindbergia* 13: 137–149.
- DURING, H. J. and B. TER HORST. 1983. The diaspore bank of bryophytes and ferns in chalk grassland. *Lindbergia* 9:57–64.
- DYER, A. F. 1994. Natural soil spore banks: can they be used to retrieve lost ferns? *Biodiversity and Conservation* 3:160–175.
- DYER, A. F. and S. LINDSAY. 1992. Soil spore banks of temperate ferns. *Amer. Fern J.* 82:89–123.
- DYER, A. F. and S. LINDSAY. 1996. Soil spore banks—a new resource for conservation. Pp. 153–160 in J. M. Camus, M. Gibby, and R. J. Johns, eds. *Pteridology in perspective*. Royal Botanic Gardens, Kew.
- ESAU, K. 1977. *Anatomy of seed plants, 2nd ed.* John Wiley & Sons, Inc., New York.
- HAMILTON, R. G. 1988. The significance of spore banks in natural populations of *Athyrium pycnocarpon* and *A. thelypteroides*. *Amer. Fern J.* 78:96–104.
- INDERJIT and K. M. M. DAKSHINI. 1995. On laboratory bioassays in allelopathy. *Bot. Rev.* 61:28–44.
- KÖPPEN, W. 1948. *Climatologia: con un estudio de los climas de la Tierra*. Trad. P.R. Hendrichs Pérez. Fondo de Cultura Economica, Mexico.
- LECK, M. A. and R. L. SIMPSON. 1987. Spore bank of a Delaware River freshwater tidal wetland. *Bull. Torrey Bot. Club* 114:1–7.
- LINDSAY, S. and A. F. DYER. 1990. Fern spore banks: implications for gametophyte establishment. *Taxonomia, Biogeografía y Conservación de Pteridófitos*. Soc. d'Hist. Nat. de les Illes Balears - IME. Palma de Mallorca: 243–253.
- LINDSAY, S., N. WILLIAMS and A. F. DYER. 1992. Wet storage of fern spores: unconventional but far more effective! *Fern Hort.*:285–294.
- MEYER, B. S., D. B. ANDERSON and C. A. SWANSON. 1963. *Laboratory plant physiology, 3rd ed.* D. Van Nostrand Company, Inc., Princeton.
- MILBERG, P. 1991. Fern spores in a grassland soil. *Can. J. Bot.* 69:831–834.

- MILBERG, P. and L. ANDERSON. 1994. Viable fern spores in an arable soil. *Fern Gaz.* 14:299–300.
- MILLER, L. E. 1994. Correlations: description or inference? *J. Agric. Educ.* 35:5–7.
- MIYAZAWA, M., M. A. PAVAN, T. MURAOKA, C. A. F. S. CARMO and W. J. MELLO. 1999. Análises químicas de tecido vegetal. Pp. 173–223 in F. C. Silva, ed. *Manual de análises químicas de solo, plantas e fertilizantes*. EMBRAPA, Brasília.
- PAGE, C. N. 1979. Experimental aspects of fern ecology. Pp. 552–589 in A. F. Dyer, ed. *The experimental biology of ferns*. Academic Press, London.
- PENROD, K. A. and L. H. MCCORMICK. 1996. Abundance of viable hay-scented fern spores germinated from hardwood forest soils at various distances from a source. *Amer. Fern J.* 86:69–79.
- PÉREZ-GARCÍA, B., A. OROZCO-SEGOVIA and R. RIBA. 1982. El banco de esporas de helechos en el suelo de los Tuxtlas, *Bol. Soc. Bot. México* 43:89–92.
- RAFFAELE, E. 1996. Relationship between seed and spore banks and vegetation of a mountain flood meadow (Mallin) in Patagonia, Argentina. *Wetlands* 16:1–9.
- RANAL, M. A. 2003. Soil spore bank of ferns in a gallery forest of the Ecological Station of Panga, Uberlândia–MG, Brazil. *Amer. Fern J.* 93:1–19.
- RATTER, J. A. 1992. Transitions between cerrado and forest vegetation in Brazil. Pp. 417–429 in P. A. Furley, J. Proctor, and J. A. Ratter, eds. *Nature and dynamics of forest-savanna boundaries*. Chapman & Hall, London.
- SCHIAVINI, I. and G. M. ARAÚJO. 1989. Considerações sobre a vegetação da Reserva Ecológica do Panga (Uberlândia). *Sociedade & Natureza, Uberlândia* 1:61–66.
- SCHNELLER, J. J. and R. HOLDEREGGER. 1996. Soil spore bank and genetic demography of populations of *Athyrium filix-femina*. Pp. 663–665 in J. M. Camus, M. Gibby and R. J. Johns, eds. *Pteridology in perspective*. Royal Botanic Gardens, Kew.
- SIMABUKURO, E. A., A. BEGOVACZ, L. M. ESTEVES and G. M. FELIPPE. 1999. Fern spore bank at Pedregulho (Itirapina, São Paulo, Brazil). *Rev. Brasil. Biol.* 59:131–139.
- SIMABUKURO, E. A., L. M. ESTEVES and G. M. FELIPPE. 1998. Analysis of a fern spore bank in Southeast Brazil. *Hoehnea* 25:45–57.
- SOUZA, G. H. M. F. and R. M. G. SILVA. 2001. Determinação do perfil fitoquímico de *Copaifera langsdorffii* Desf. (Caesalpiniaceae). III Simpósio Brasileiro de Farmacognosia. Sociedade Brasileira de Farmacognosia. Setembro, Curitiba, Paraná, Brasil: QN-26 (Abstract).
- STRICKLER, G. S. and P. J. EDGERTON. 1976. Emergent seedlings from coniferous litter and soil in Eastern Oregon. *Ecology* 57:801–807.
- WEE, Y. C. 1974. Viable seeds and spores of weed species in peat soil under pineapple cultivation. *Weed Research* 14:193–196.